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Violet hybrids between species of the palmata group

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(WITH PLATES 5–7)

In my last paper on violet hybrids, published over six years ago, and in the one preceding it,* I described only one hybrid whose parents were both in the natural group represented by *Viola palmata*. I recognized the fact, however, that these closely allied species seemed "to be confluent when growing together," and stated my belief that "they can and do interbreed." It has been often observed that natural hybrids between doubtfully distinct species, or between a species and its variety, are the most difficult to determine with certainty; the less remote from each other the two species that hybridize, the less marked and less numerous are the signs of hybridity in the offspring. For six seasons now, I have had many suspicious intermediates of this group under cultivation, raising sometimes a hundred or more offspring from one plant, extending through three or four generations. Some of the results of these experimental cultures, I trust, will prove of interest to students both of systematic botany and of heredity.

VIOLA PALMATA × PAPILIONACEA Brainerd.†

Leaves cordate-ovate as in *V. papilionacea*, lobed after the manner of *V. palmata*, but less deeply so; the capsules from cleistog-

* Rhodora **6**: 213–223. N 1904; and Rhodora **8**: 49–60. Mr 1906.

† Dowell, Ph. The violets of Staten Island. Bull. Torrey Club **37**: 177. Ap 1910. At least one of the specimens there cited (*4777*), Dr. Dowell would now call *V. papilionacea* × *triloba*.

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amous flowers ovoid-conical, 5–7 mm. long, or half as long as the normal capsule in either parent, containing in the 48 capsules examined an average of 4½ seeds to the capsule. (PLATE 5, *Aa*.)

In June 1906 Mr. W. DeWitte Miller sent me from Plainfield, N. J., a plant that he considered this hybrid. Three years after transplanting, the rootstock was much branched and 8–10 inches broad; in the spring of 1909 part of it was broken up and ten new plants obtained, which in a year or two became so luxuriant that half of them were purposely destroyed. From the original plant 23 offspring have been raised. Of these, 6 had deeply lobed leaves like those of *V. palmata;* 4 had uncut leaves like those of *V. papilionacea;* and the remaining 13 had leaves somewhat lobed as in the hybrid. (See PLATE 6.) In 1909 numerous offspring were raised from 8 of the above 23 plants, with the following results: (1) The seedlings from a plant with uncut leaves (in one instance 18) had always uncut leaves like the parent. (2) The seedlings from a plant with deeply cut leaves (in one instance 19) had always deeply cut leaves like the parent. (3) The seedlings of plants with leaves somewhat lobed as in the original hybrid, in the five instances tested, always gave plants of the three forms given by the original hybrid. In more technical language, the form of the hybrid leaf displays no dominance of the form of either parent but is a compromise between the two forms. But when plants having this hybrid form of leaf reproduce, the offspring present variously the two extreme forms of the original species and the compromise form of the hybrid, in this conforming to the Mendelian law of 'segregation.'

There is also approximate conformity to the Mendelian ratio of 1:1:2 in the number of each of the three kinds of offspring. The total progeny raised from plants having the hybrid form of leaf was 49; of these, 13 had deeply cut leaves (form *A*); 12 had uncut leaves (form *a*); and 24 had the compromise leaf (form *Aa*). This is as near to the above ratio as is practically possible with a total of 49 plants.* The further Mendelian principle is illustrated: that when an offspring of a hybrid reverts to a pure character of either parent species, that character continues pure in succeeding generations if the plant is self-fertilized. In this

* The theoretical ratio 12¼ : 12¼ : 24½ cannot be concretely realized, as the number of each kind of hybrid forms must necessarily be a whole number.

particular hybrid, when the leaf form of *V. papilionacea* once reappears, it is kept up in the subsequent progeny; so, when the leaf form of *V. palmata* once comes back, it comes to stay.

Another instance of a cross between *V. palmata* and *V. papilionacea* was found among several plants of *V. palmata* from Orange, N. J., exhibited by Miss Angell at the "violet symposium" at Bronx Park, May 1905. The plants were later set out in the New York Botanical Garden. On examining them the following September, my attention was called to a stocky plant with leaves wider and less deeply lobed than the rest; cleistogamous flowers were abundant, but their capsules were nearly sterile. From the few ripe seeds obtained, plants were propagated for three generations, with results quite the same as in the hybrid from Plainfield.

In the autumn of 1906 I received from Miss A. M. Ryan of New London, Conn., fresh leaves and a few ripe seeds of a plant collected by Miss Pauline Kaufman in the vicinity of New York City. The leaves were quite the same as those of Mr. Miller's hybrid. Two plants only were raised from the seeds sent; but later, a brood of offspring from each of these. The first brood (sowing 320) consisted of nine heterogeneous plants, proving the hybrid nature of the mother, as well as of the plant collected by Miss Kaufman. Of the second brood (sowing 592) eight plants were raised, all with deeply lobed leaves like the mother, and hardly distinguishable from normal *V. palmata* except by smaller capsules and greatly impaired fertility.

I have said nothing as yet of the inheritance in these hybrids of pubescence from *V. palmata*, or of the lack of it from *V. papilionacea;* this, however, was quite similar to the inheritance of lobation, or the lack of it, though not as conspicuous. The most interesting circumstance was that frequently the lobed leaves and the pubescence of *V. palmata* were not both inherited by the same offspring. A seedling with lobed leaves would often be glabrous; and on the other hand, one with uncut leaves would often be pubescent and might have easily passed for *V. sororia* except for its infertility.

Such aberrant forms occasionally appear in the wild. In May 1909 I saw some excellent photographs taken by Miss E. M. Kittredge of certain anomalous violets found near her home in

Spring Valley, N. Y. One showed plainly a glabrous specimen of *V. palmata* in flower. By the kindness of Miss Kittredge the live plant was presented to me in June. On collecting close-fertilized seeds the following August, I found on the average 16 seeds to the capsule; that is, about three fourths of the ovules were undeveloped. Among the offspring raised the following season, were plants representing not only the deeply lobed leaves of *V. palmata* but also the uncut leaves of *V. papilionacea*. Both forms, however, were glabrous, as was to be expected; for a dominant character like pubescence, when once lost, never reappears. Nevertheless, the hybrid origin of the wild plant was clearly established. Let me cite one further instance.

On April 15, 1909, I found at Tryon, N. C., what seemed to be a colony of this glabrous *V. palmata*. In the vicinity grew both the normal hairy *V. palmata* and the glabrous *V. papilionacea*. Of the anomalous plants six with leaves moderately lobed were shipped to Vermont to be grown and studied in the garden. All proved to be more or less infertile, averaging about 20 seeds to the capsule. Offspring were raised from all six; and in each brood but one were to be seen plants with uncut leaves, indicating that one parent of the original hybrid was *V. papilionacea;* from which, doubtless, was also inherited the glabrous character of the plants at Tryon.

Viola palmata × **triloba** hyb. nov.

First 1–3 leaves of spring often uncut as in *V. triloba*, followed by others more or less 5–7-lobed, much like those of *V. palmata* but the basal lobes broadly dilated and coarsely toothed as in *V. triloba;* later leaves less dissected, mostly 3-lobed or obscurely lobed; capsules infertile, about one third of the ovules maturing into seeds; offspring multiform, often bearing on the middle segment of the trilobed leaves 4–8 undulations or coarse teeth.

The genuine *V. Angellae* Pollard (Torreya **2**: 24. 1902), proves to be this hybrid, as the original description and the type sheet of mature plants (U. S. National Herbarium no. 352,093) clearly show. One of the flowering plants on sheet no. 364,862 may, however, be pure *V. palmata*. It would seem that the original collection by Miss Angell, June 1899, contained many specimens of *V. palmata*, as some of them are to be seen mounted

in the National Herbarium, and others were distributed only last summer with the name "*V. Angellae*" on the printed labels. Possibly some of these plants may be imperfect reversions to *V. palmata*. Furthermore, as already stated, most of the specimens of "*V. Angellae*" exhibited at Bronx Park May 1905 were *V. palmata*. Others also have erroneously assumed that plants that they collected at the type station were therefore typical *V. Angellae*. Mr. Pollard distinctly states that his new species is associated with *V. palmata* in the Orange Mountains.

In May 1908 Dr. E. L. Greene kindly sent me a dozen plants of his *V. variabilis* from the type station, opposite Harpers Ferry and named by him Maryland Heights. Most of these plants have since been growing in the garden, and from some of them have been raised two generations of offspring. These plants I make out to consist of two different hybrids of *V. triloba*, one being the *V. palmata* × *triloba* above described. A close comparison of the characteristic leaf of this hybrid (PLATE 7, FIG. 3 and 4) with the leaves of the supposed parents (FIG. 1 and 2) will disclose its compromise outline. The leaves of Dr. Greene's plant, though at first suggesting *V. palmata*, differ in having the broad basal lobes of *V. triloba* even as early as May 31; while specimens collected July 22 and September 16 display leaves decidedly trilobed, and some hardly lobed at all. This tendency towards uncut leaves in autumn is characteristic of *V. triloba* but not of *V. palmata*. Furthermore, in some of the segregating offspring (PLATE 7, FIG. 5 and 7) may we not see in the oddly shaped middle segment the resultant of opposite impulses, one demanding 9–11 lobes, the other forbidding more than 3?

So much for the evidence from the living plant, cultivated for four seasons and through three generations. The conclusion drawn from this experiment is well sustained by a careful study of the seven sheets of "*V. variabilis*" at the National Museum. Four were collected May 14, 1898—two by Dr. Greene, and two by Mr. Pollard, who accompanied him—and three others by Dr. Greene May 10, 1903; all from Maryland Heights opposite Harpers Ferry. The 17 plants here mounted I regard as a medley of at least five distinct forms, three of which are represented in the live plants sent in 1908. I shall here speak of only

the palmatifid form, which Dr. Greene says "is exceedingly similar to Mr. Pollard's recently proposed *V. Angellae*, indeed so much like it that I have little if any doubt they are one, specifically."* In this I agree with Dr. Greene; and in both cases plants of pure *V. palmata* were collected with the hybrid *V. palmata* × *triloba*, three of the former and four of the latter appearing among the 17 mounted specimens labeled by Dr. Greene *V. variabilis*. One of each kind is to be seen on U. S. National Herbarium sheet no. 328,245, collected by Mr. Pollard and labeled by him in pencil "*V. palmata*."

A plant distributed by Mr. Witmer Stone, as *V. palmata variabilis* (Greene),† seems to be, at least in part, the hybrid under discussion. I have observed also several other specimens that appear to be this; but one may not with confidence identify a hybrid between two species so closely allied without abundant material or the data obtained by experimental cultures.

Viola papilionacea × triloba hyb. nov.

Leaves of late spring and summer shallowly, often obscurely, 3–5-lobed, uncut leaves subcordate, often broadly reniform; capsules even from cleistogamous flowers infertile; offspring inheriting diversely the opposed characters of the parent species.

My first acquaintance with this hybrid was through some anomalous living plants sent from Washington, D. C., in May 1906, by Mr. E. S. Steele, along with samples of pure *V. triloba*. The six plants of the latter were quite alike—pubescent, cut-leaved, buff-seeded, fertile, and easily separated by the purple tinge of the early spring foliage from the anomalous plants. These were of three forms: (1) One plant fairly fertile, with pubescent uncut leaves as in *V. sororia* but bearing buff seeds. (2) Two plants fairly fertile, with uncut leaves and dark brown seeds as in *V. papilionacea* but pubescent. (3) One plant nearly sterile, averaging 6½ brown seeds to a capsule, the leaves glabrous and somewhat 3-lobed. Offspring were raised from all of these: those from (1) and (2), 6 plants from each, seemed to be stable, that is, in each instance all had characters like those of the mother; the offspring from (3) were only two, one with uncut leaves, one with 3-lobed leaves.

* Pittonia 5: 91. 1902.

† No. *5111*, colony 5, Argus, Pa., June 8, 1903, Dr. C. D. Fretz.

The problem is to account for the presence in a colony of normal *V. triloba* of three plants so variant from *V. triloba* and from each other. But however confused the situation may appear, all may be accounted for by regarding the three odd plants as the descendants of a cross between *V. triloba* and *V. papilionacea*, a common species of the region. Plant (1) seems to have escaped the conflict of characters forced into the make-up of the original hybrid and attained to stability and relative fertility, inheriting uncut leaves from *V. papilionacea* but pubescence and buff seeds from *V. triloba*. Plant (2) seems to be another stable ex-hybrid, inheriting also pubescence from *V. triloba* but dark brown seeds as well as uncut leaves from *V. papilionacea*. Plant (3) is partly rescued from hybrid instability, at least as regards pubescence, but is still hybrid as regards leaf form — what we may call a subhybrid, still bearing in its infertility the stigma of its irregular parentage.

Of the twelve plants of "*V. variabilis*" sent me by Dr. Greene in 1908 I regard nine as the progeny of *V. papilionacea* × *triloba;* and the case is exactly parallel to the one just described, though on a somewhat larger scale. The differing characters of Dr. Greene's plants are presented in the following synopsis, and will be found in all cases to be only new combinations of those found in the putative parents. The numbers given are those that the several plants bear in my notebook.

Leaves with uncut blades.
  Blades broadly cordate-ovate, blunt-pointed, pubescent beneath.
    Seeds buff, about 11 in a capsule 2, 12
    Seeds dark brown, about 14½ in a capsule 5, 6, 7, 10
  Blades much dilated, subglabrous; seeds brown 4
Leaves slightly lobed in spring, later leaves uncut, broadly reniform, truncate or subcordate; seeds brown 9
Leaves 3–5-lobed, subglabrous; seeds brown 8

On the seven sheets of "*V. variabilis*" in the U. S. National Herbarium there are only six plants that represent this group, and they all have uncut leaves. As none were collected later than May 14, the color of their seeds is unknown; nor has any plant developed leaves with subcordate reniform outline. These forms and the two with lobed leaves (no. 4, 9, and 8 above) indicate that Dr. Greene sent me a fuller representation of this hybrid group than he had previously collected for himself.

Dr. Greene's conception of a species, which without hybridizing appears "under forms enough to make three," is quite contrary to the latest inductions of biology. The law that "like produces like," even through seed (when pure or not affected by foreign pollen), is confirmed by numerous experimental tests. If we except the extremely rare cases of observed mutation, the offspring of a species or of a natural variety is always uniform.* Whenever a miscellaneous offspring appears, we may be confident that at no very remote past, species or varieties, as unlike or more unlike than the offspring, were sexually united in the parentage.†

Several other examples of *V. papilionacea* × *triloba* might be cited, but I name only two from well known collections: No. 34, North American Violaceae, Greene and Pollard; "*V. palmata dilatata* Ell." New Springville, Richmond Borough, N. Y., Wm. T. Davis, July 17, 1903; also no. *5108*, colony 3, Violets of Philadelphia and vicinity; "*V. palmata dilatata* Ell." Sherwood, Pa., June 17, 1903.

Viola sororia × **triloba** hyb. nov.

The confluence of these two species is generally recognized, and it is so common that many students of *Viola* have regarded them as forms of the same species; just as, because of a similar confluence, *V. sagittata* has been held to include *V. fimbriatula*. The shallow and obscure lobes of the hybrid leaf are the same as in *V. papilionacea* × *triloba*, but the foliage is never glabrous. But more satisfactory than this negative test is the discovery of the intermediate forms in a region from which *V. papilionacea* is absent. Along a shady limestone ledge in Orwell, Vt., where *V. triloba* and *V. sororia* were abundant, but no *V. papilionacea*, was found in 1904 a large colony of intermediates that will pass muster as *V. sororia* × *triloba*. In this case the most satisfactory evidence would come from the artificial production of the hybrid; this I trust will soon be attempted.

* Dimorphism, such as the constant reproduction of both staminate and pistillate plants, or of long-styled and short-styled forms, belongs to another class of phenomena.

† See DeVries, H. Species and varieties. Lectures 6 & 7, on stability and vicinism.

It may be noted that the leaf outline in *V. triloba* is relatively broader and less deeply cordate than in *V. sororia* (or in *V. papilionacea*), and that the hybrid offspring may inherit the uncut leaves of the latter and the broad outline of the former, thus presenting a decidedly reniform leaf. Such stable forms often emerge in experimental cultures and are occasionally met with in the wild near stations for *V. triloba*. I have usually found such broad-leaved specimens of "*V. sororia*" to be infertile. It seems to be this that Dr. Greene has named *V. populifolia*. (Pittonia **3**: 337. S 1898.)

The two hybrids of *V. Stoneana* that follow are analogous to the two last described.*

Viola papilionacea × **Stoneana** hyb. nov.

Glabrous; first one or two leaves uncut, succeeded by larger ones 5–7-lobed; the middle segment broad, the basal lunate coarsely serrate, the lateral but slightly if at all narrowed at the base; autumn leaves often much dilated and obscurely lobed; capsules more or less infertile, 7–12 mm. long; offspring diversiform as to lobation.

A plant of this was taken from Ivy Hill Cemetery, Philadelphia, September 1905. From close-fertilized seed collected and sown in the autumn of 1906 were grown the following season, plants that had three distinct leaf forms: (1) the uncut leaf of *V. papilionacea;* (2) the 5-parted leaf of *V. Stoneana* with segments much narrowed toward the base; (3) the 5-lobed leaf of the original plant. From six of these plants a third generation was grown in 1909, in which all from (1) and (2) were homophyllous, and those from (3) heterophyllous, as in the brood obtained in 1907. From (1) a fourth generation was raised in 1910, all like the parent.

Viola Stoneana × **triloba** hyb. nov.

Leaves 5-lobed; lower surface and petioles somewhat pubescent; capsules infertile; seeds buff; offspring in part glabrous, in part quite pubescent.

The original plant was collected at Ivy Hill Cemetery, Philadelphia, in 1905, with the one last described. Four seedlings

* Cf. The evolution of new forms in *Viola* through hybridization. Am. Naturalist **44**: 231. Ap 1910.

were grown in 1907: one quite glabrous, in this reverting to *V. Stoneana;* the other three more or less pubescent. From each of the four plants offspring were obtained in 1909. Those from the glabrous plant were also all glabrous; two of the pubescent plants bore both pubescent and glabrous offspring; the remaining pubescent plant bore nine offspring, all pubescent, thus indicating that in this instance the pubescence of the mother plant was a stable character. This happens to be exactly the relative number of these three forms of offspring required, on the average, by the laws of Mendel.

Viola latiuscula × triloba hyb. nov.

Leaves moderately 3–5-lobed, sparsely pubescent on the petioles and veins of the young leaves; capsules about 8 mm. long, maturing 10 or 12 brown seeds; progeny heterogeneous.

For my acquaintance with this hybrid I am indebted to the discernment and diligence of Mr. B. H. Slavin of the Park Department of the City of Rochester, N. Y. On June 19, 1909, he sent me from Salamanca, N. Y., six odd-looking plants, all glabrous; four with leaves somewhat lobed, subcordate-ovate, blunt-pointed; two with leaves uncut. As they flowered and matured the following season, I detected certain marks of *V. latiuscula:* a crimson tinge in the early spring foliage, and a granular roughness along the upper edges of the petiole. At my request Mr. Slavin revisited the station for further collections July 6, 1910, and sent me in the autumn an excellent suite of the various forms to be seen in that colony. For a better apprehension of their relation to each other, I borrow some of the symbolism of Mendel. For brevity he uses letters instead of phrases, somewhat in this fashion:

Let A = cut-leaved	Let B = pubescent
" a = with leaves uncut	" b = glabrous
" Aa = with leaves somewhat uncut	" Bb = somewhat pubescent

All of these six characters are found in the above described hybrid or in the parent species; in the offspring of the hybrid they should be redistributed in all possible combinations. It is evident that each one of the three characters in the first group may combine with each of the three in the second group, making in all nine different combinations. These are given in the following table,

the asterisk after any form denoting its occurrence at the Salamanca station.

1	A	B	*	Reversion to typical *V. triloba*.
2		b	*	New and stable form, glabrous *V. triloba*.
3		Bb	*	Cut-leaved form, hybrid as respects pubescence.
4	a	B	*	New and stable form, pubescent *V. latiuscula*.
5		b	*	Reversion to typical *V. latiuscula*.
6		Bb		
7	Aa	B	*	Pubescent form, hybrid as respects lobation.
8		b	*	Glabrous form, hybrid as respects lobation.
9		Bb	*	Dihybrid, *V. latiuscula* × *triloba*.

The one form lacking should be a somewhat pubescent plant with uncut leaves. The proof that we have here a colony of *V. latiuscula* × *triloba* will be convincing to one familiar with the behavior of hybrids.

Three hybrids of *V. hirsutula*, one with each of our three cut-leaved species, call for a few brief comments.

Viola hirsutula × triloba nom. nov.

V. palmata × *villosa* Brainerd, Rhodora **8**: 56. Mr 1906. Cf. House, H. D. Violets of the District of Columbia, Rhodora **8**: 121. Jl 1906. The former name of each parent species has proved to be untenable.*

This beautiful and easily recognized hybrid is of frequent occurrence from northern New Jersey to the mountains of North Carolina and eastern Tennessee. A most interesting colony, of a hundred or more plants, was found at Morristown, Tenn., on a tract of woodland recently cleared and worked to be made an addition to a cemetery. The plants were reverting in various ways to the characters of one or the other of the original parents. Some were large in size, others small; some had lobed leaves, others not; most had both the silvery pubescence of *V. hirsutula* on the upper surface of the leaf and the villous pubescence of *V. triloba* on the lower surface of the leaf, but occasionally one or the other form of pubescence was nearly or quite lacking. Not only from these, but from a plant sent me October 1907 from Orange, N. J., by Miss A. M. Ryan, I have raised unlike offspring, some with uncut leaves, some with leaves mostly lobed. In Mr.

* See Rhodora **9**: 96–98. Je 1907; and Bull. Torrey Club **37**: 584–587. D 1910.

Witmer Stone's Violet Distribution no. *5107*, colony 3, "*V. palmata dilatata* Ell.," Sherwood, Philadelphia, May 17, 1903, is plainly this hybrid. So also is *H. D. House 823*, Glen Echo, May 25, 1905, Violets of the District of Columbia. The name on the label, "*V. villosa* × *palmata asarifolia*" would indicate that Mr. House considered it *V. hirsutula* × *sororia;* but my specimen bears one *lobed* leaf.

Viloa hirsutula × **palmata** hyb. nov.

Plant small, cespitose; leaves all palmatifid, the incisions becoming shorter toward the base; the blades somewhat pubescent beneath, finely ciliate and bearing minute white hairs along the veins above; capsules nearly sterile.

One plant only was found in an open woods near Plainfield, N. J., September 1906, with both parents growing near. This was transplanted to the Middlebury garden and later multiplied by division, but I have failed to obtain sufficient seeds for a sowing. However, the marks of its double parentage are pronounced.

Viola hirsutula × **Stoneana** nom. nov.

V. Stoneana × *villosa* House, Rhodora **8**: 121. *pl. 72.* Jl 1906. The plants seem to be rare; Mr. House got it only from the type station, Hyattsville, Md. I collected a specimen at Ivy Hill Cemetery, Philadelphia, Sept. 6, 1905; and in April 1908 Dr. Theo. Holm kindly sent me a live plant from Brookland, D. C. From the latter plant I obtained in 1909 three offspring that differed widely from each other in the relative number of cut and uncut leaves, and in that the cut leaves of the several plants were quite unlike each other in the number and length of the lobes.

In two of the ten hybrids discussed in this paper, both parents are cut-leaved species: *V. palmata* × *triloba* and *V. Stoneana* × *triloba;* in the remaining eight the leaves of one parent are cut, of the other uncut. In all cases the leaf of the first hybrid (F_1) has an intermediate form. This rule regarding hybrid leaf form holds in all observed cases in the genus *Viola*. The same rule prevails to a large extent as regards pubescence; but here there are also cases of more or less complete dominance, as in *V. Stoneana* × *triloba*, where it is impracticable without an experimental test to distinguish among pubescent offspring which is stable

and which unstable. Even in the character of seed color, or of capsule color, Mendelian dominance of brown over buff, or of purple over green, is usually somewhat imperfect; so that after some practice one can distinguish fairly well between pure and hybrid dominants. Details of this behavior will be given in a further paper, on the hybrids of *Viola pedatifida* of the Middle West.

MIDDLEBURY, VT.

Explanation of plates 5-7

PLATE 5

⅔ natural size

Aa. *Viola palmata* × *papilionacea* Brainerd, transplanted from Plainfield, N. J., June 1906; ex horto, Middlebury, Vt., Sept. 6, 1909.

A. Leaf of *Viola palmata* L., Yonkers, N. Y., Sept. 9, 1905.

a. Leaf of *Viola papilionacea* Pursh, Plainfield, N. J.

PLATE 6

⅔ natural size

Three offspring in third generation of *Viola palmata* × *papilionacea* shown in PLATE 5, *Aa;* grown from close-fertilized seeds of one plant. Ex horto, Oct. 2, 1909.

A. Reverting to *V. palmata* L.

a. Reverting to *V. papilionacea* Pursh.

Aa. Repeating hybrid leaf form.

PLATE 7

⅔ natural size

1. Leaf of *V. palmata* L., Orange, N. J.

2. Leaf of *V. triloba* Schwein., New Haven, Conn.

3 and 4. Two leaves, lower surface and upper, of *V. palmata* × *triloba*, transplanted from Maryland Heights, Md., May 1908; ex horto, May 31, 1911.

5–7. Three leaves of offspring of hybrid in third generation, grown from close-fertilized seeds of one plant.

Studies on the Rocky Mountain flora—XXVI

PER AXEL RYDBERG

PINACEAE and JUNIPERACEAE

In the New Manual of Botany of the Central Rocky Mountains no reference is made to *Picea canadensis*, although it has been collected in the Black Hills of South Dakota and Wyoming. Blankinship in his supplement to the Flora of Montana,* reports *P. alba*, which is the same, from four localities in Montana. This, however, I think is erroneous. All specimens from Alberta, British Columbia, and Montana, that I have seen determined as *P. canadensis* or *P. alba*, belong to *P. albertiana* S. Brown. Probably the specimens reported by Blankinship belong there also. *Abies grandis* is also omitted in the New Manual. This is not uncommon in Montana west of the continental divide. Perhaps that part of the state is not intended to be included in the range covered by the New Manual, as it includes only "most of Montana." The species has been reported from the Yellowstone Park, but the reference is uncertain. Blankinship, loc. cit., also reports *Juniperus virginiana* from Montana and cites three localities. I have no evidence that the determinations were correct nor have I seen any specimens from the state. What makes me more doubtful as to the correctness of the determination is that two of the localities are situated west of the continental divide, and at Bozeman, the third locality, I have myself collected during parts of three summers and have not seen it.

I doubt very much if *Juniperus Knightii* A. Nelson can be upheld as a species distinct from *J. utahensis* (Engelm.) Lemmon. The characters given, apparently do not hold. The leaves are supposed to be 2-ranked in *J. monosperma* and *J. utahensis* and 3-ranked in *J. Knightii*. I know that in the first two they are both 2- and 3-ranked. I have not seen the type of *J. Knightii*, but in a specimen distributed under that name by Professor Nelson

* Montana Agr. Coll. Sci. Stud. Bot. 1: 39. 1905.

himself the leaves are both 2- and 3-ranked on different twigs of the same branch. The seeds in *J. utahensis* are either obtuse or acutish at the apex, and these characters do not furnish any distinction. I have spoken to Dr. J. A. Shafer, who helped Dr. N. L. Britton in preparing North American Trees, and he told me that he had come to exactly the same conclusion as I.

The following two changes in the nomenclature seem to be advisable.

Hesperopeuce Mertensiana (Bong.) Rydb. comb. nov.

Pinus Mertensiana Bong. Mem. Acad. Sci. Nat. St. Petersb. VI. **2**: 163. 1832.

Abies Mertensiana Lindl. & Gord. Journ. Hort. Soc. Lond. **5**: 211. 1850.

Abies Pattoniana Jeffrey; A. Murray, Rep. Oregon Exped. 1. 1853.

Tsuga Pattoniana Sénéc. Conif. 21. 1867.

Hesperopeuce Pattoniana Lemmon, Rep. Calif. State Board Forestry **3**: 126. 1890.

Tsuga Mertensiana Sargent, Silva **12**: 77. 1898. Not *T. Mertensiana* Carrière, 1867.

I agree fully with Mr. Lemmon that this species should be removed from *Tsuga*. Both its cones and its leaves are more like those of a spruce than those of a hemlock, and the habit of the tree is different from both. Mr. Lemmon, however, did not adopt the oldest available specific name.

Sabina horizontalis (Moench) Rydb. comb. nov.

Juniperus horizontalis Moench, Meth. 699. 1794.

Juniperus prostrata Pers. Syn. **2**: 632. 1807.

Juniperus Sabina procumbens Pursh, Fl. Am. Sept. 647. 1814.

Sabina prostrata Antoine, Cupress. Gatt. 57. 1857–70.

EPHEDRACEAE

Marcus E. Jones* reduced *Ephedra viridis* Coville to a variety of *E. nevadensis*. I do not know exactly what *E. viridis* is, as I have not seen the type, but the Utah plant which Jones had in mind, does not seem to agree with the description. We have duplicates of some of the numbers cited by Jones, and these seem to be typical *E. nevadensis*.

* Proc. Calif. Acad. II. **5**: 726. 1895.

SPARGANIACEAE

Sparganium simplex L. has been reported again and again from the Rocky Mountains, but all the specimens I have seen under that name belong either to *S. longipedunculatum* (Morong) Rydberg or to *S. angustifolium* Michx. *S. longipedunculatum* resembles *S. simplex* much in habit but is usually more slender, and the leaves are not so triangular-keeled as in that species. The main difference is, however, in the shorter style and stigma. *S. simplex* is very rare in the United States. I have seen specimens only from the State of Washington. It is otherwise found in British Columbia and along the St. Lawrence River in Ontario and Quebec.

ZANNICHELLIACEAE

Potamogeton perfoliatus is not found in the Rocky Mountain region. It is there represented by *P. Richardsonianus*. Notwithstanding the fact that N. Taylor includes the latter in the former, I am convinced that they are distinct. This opinion is based on field studies. My contentions are also supported by M. L. Fernald.

I cannot find any specific distinctions between *Ruppia curvicarpa* A. Nels. and *R. maritima* L. The length of the pedicels is merely a matter of age and other conditions; the typical *R. maritima* has strongly oblique fruit, gibbous at the base as described in *R. curvicarpa;* slender or stout, straight and curved styles are found in the same individual even. Taylor, also, could find no distinctive characters.

ALISMACEAE

Alisma Plantago-aquatica L. is not found in America. In this European species the achenes have different beaks from those found in the North American species. The common species of the Rocky Mountain region should be known as *A. brevipes* Greene. *Alisma Geyeri* Torr. is also found in the regions. (See my Flora of Montana.) It has been collected later in Utah.

Blankinship* described one new species and one new variety of *Sagittaria*. *S. paniculata* Blank. is but a well developed *S.*

* Loc. cit. 40.

arifolia Nutt.,* and *S. arifolia tenuior* is but a depauperate form of the same. Both *S. paniculata* Blank. and *S. arifolia* Nutt. have to give way for the older name *S. cuneata* Sheldon,† which was described from the deep-water form of the same species.

POACEAE

Blankinship reported *Panicum nitidum* Lam. from Columbia Falls, Montana. This must be an error, for that species is known only from the eastern seaboard from southern Virginia to eastern Texas. *Aristida fasciculata Hookeri* of Blankinship's list is the same as *A. longiseta*.

Professor Nelson reports *Aristida oligantha* from Colorado. I have seen no specimens from that state and none from west of central Nebraska. Perhaps *A. bromoides* might have been mistaken for it.

The oldest available specific name for *Eriocoma cuspidata* is *hymenoides*, which is therefore adopted, and its name and synonymy is as follows:

Eriocoma hymenoides (R. & S.) Rydb. comb. nov.

Stipa membranacea Pursh, Fl. Am. Sept. 728. 1814. Not *S. membranacea* L. 1753.

Stipa hymenoides R. & S. Syst. **2**: 339. 1817.

Eriocoma cuspidata Nutt. Gen. **1**: 40. 1818.

Oryzopsis cuspidata Benth.; Vasey, Special Rep. U. S. Dept. Agr. 63: 23. 1883.

The following species of *Muhlenbergia* should be added to the flora of the Rocky Mountain region: *M. pauciflora* Buckl. (*M. neomexicana* Vasey; *M. Pringlei* Scribn.), *M. polycaulis* Scribn., and *M. curtifolia* Scribn., which were collected by Professor A. O. Garrett and myself in southeastern Utah last summer. *Alopecurus fulvus* Smith is not found in America, except perhaps in Greenland. *A. aristulatus* Michx. is not the same, differing not only in the general habit, not being depressed-geniculate, but also in the different position of the awn of the floral glume. *Alopecurus pallescens* Piper has been collected in both Idaho and Montana.

* J. G. Smith. Rep. Missouri Bot. Gard. **6**: 32. 1894.

† Bull. Torrey Club **20**: 283. 1893.

Professor Nelson, in the New Manual, includes *Sporobolus vaginaefolius* and *Cinna arundinacea*, which I think are erroneously reported for the region.

The following species of *Calamagrostis* have to be included in the Rocky Mountain flora: *C. Vaseyi* in Montana, *C. rubescens* and *C. lucida* in Wyoming.

Professor Nelson reduced *Avena americana* to a synonym of *A. Mortoniana*. I think they are distinct, but if united, they should bear the name *Avena Hookeriana*, an older name for the former. *Arrhenatherum elatius* has been collected in Colorado, and *Danthonia spicata* is common in the Black Hills.

Deschampsia pungens sp. nov.

A densely tufted perennial; stem 3–4 dm. high, glabrous and shining; basal leaves numerous, the old subchartaceous sheaths from preceding season remaining, strongly striate, glabrous, often slightly tinged with purplish; ligules triangular-lanceolate, 4–5 mm. long: blades spreading, more or less arcuate, strongly involute, bluish green or in age straw-colored, strongly striate, minutely scabrous-pruinose, stiff and with a callous pungent point; stem leaves few; blades 2–5 cm. long, similar; panicle open, branches in age spreading; peduncle and its branches more or less purplish, glabrous or minutely scabrous; empty glumes subequal, 3.5–4.5 mm. long, lanceolate, acute, purple, with scarious margins; rachis long-hairy; floral glumes 3–3.5 mm. long, similar to the empty glumes; awn attached near the base, equaling or barely exceeding the floral glume.

This species is closely related to *D. caespitosa* but differs in the stiff, involute, pungent-pointed leaves and in the position of the dorsal awn of the floral glumes. This is attached near the base of the glume, while in *D. caespitosa* it is attached one fourth or one fifth the distance from the base. It grows near hot springs.

ALBERTA: Along stream below warm sulphur springs, vicinity of Banff, July 10, 1899, *McCalla 2309* (type in herb. N. Y. Bot. Gard.).

WYOMING: Lower Geyser Basin, Yellowstone Park, August 4, 1897, *Rydberg & Bessey 3590*.

Chloris brevispica Nash has been collected at Wray, Colorado, and *Blepharidachne Kingii* (S. Wats.) Hackel (*Eremochloa Kingii*

S. Wats.) in eastern Utah, *Eragrostis lutescens* Scribn. and *E. hypnoides* Nees in Idaho, *E. secundiflora* Presl in Colorado, and *E. neomexicana* Vasey in southern Utah. *Briza maxima* L. has become introduced in Colorado.

Poa Multnomae Piper and *P. ampla* Merrill have been collected in Montana since 1909. *Poa flava* L. is not a *Poa* at all, as shown by Professor A. S. Hitchcock, and the name to be used for *P. serotina* Ehrh. is *P. triflora* Gilib. *Poa laxa* Haenke is not found in the Rocky Mountains, and what has been masquerading under that name is *P. alpicola* Nash. *Poa paddensis* Piper is an older name for *P. subpurpurea* Rydb., both being based on *P. purpurascens* Vasey. In the New Manual no reason is given why *P. Buckleyana* Nash, published in 1895, should be used instead of *P. Sandbergii* Vasey of 1893. They may be the same. *P. Buckleyana* Nash was a substitute for the untenable *P. tenuifolia* Buckl., while *P. Sandbergii* was described independently. I have not seen Buckley's type, but it is supposed to have been based upon the manuscript *P. tenuifolia* Nutt. Dr. A. Gray accused Buckley of having pilfered the species from Nuttall. There is in the herbarium of the New York Botanical Garden a specimen named by Nuttall *P. tenuifolia*, and this specimen belongs to *P. Sandbergii*. What has usually passed under the names *P. tenuifolia* and *P. Buckleyana* is different, and I think represents a distinct although closely related species. The grass common in Wyoming and Colorado belongs to this and not to the typical *P. Sandbergii*, which ranges only west of the continental divide.

Although *Poa pseudopratensis* Scribn. & Rydb. resembles the common bluegrass in habit it is entirely distinct from it and more closely related to *P. arida* Vasey. Like that species it lacks the cobweb at the base of the floral glumes altogether, while *P. pratensis* has the best developed cobweb of all our species. Likewise *P. phoenicea* Rydb., also cited as a synonym under *P. pratensis* in the New Manual, has no cobweb and belongs in another section of the genus. I am inclined to think that *P. phoenicea* Rydb. is the same as the original *P. Grayana* Vasey, while *P. Grayana* of my Flora of Colorado is a large-flowered *P. Pattersonii* or a closely related species.

Poa crocata Michx. is the same as *P. caesia strictior*. In the

Torrey Herbarium there are a few spikelets of *P. crocata* Michx., and I have seen the type of *P. caesia strictior*. The plant is the most common species that has been known under the name *P. nemoralis* in the Rockies. It is intermediate between *P. interior* Rydb. and *P. rupicola* Nash, in habit resembling more the latter, but the cobweb is present.

In the New Manual of Botany of the Central Rocky Mountains, *Poa Tracyi* Vasey, *P. flexuosa occidentalis* Vasey, *P. occidentalis* Rydb., and *P. callichroa* Rydb. are given as synonyms under *P. nervosa* (Hook.) Vasey. In *P. callichroa* the cobweb is present, and that species is related to *P. arctica* although much larger. In the rest the cobweb is wanting. The plant described by Professor Nelson is *P. occidentalis* (Vasey) Rydb. If *P. Tracyi* Vasey is the same I do not know, but *P. nervosa* (Hook.) Vasey is a different plant. A duplicate of the type is in the Torrey Herbarium. In this species the glumes are very thin and the nerves very prominent, stronger than in any other species of *Poa* known to me.

Poa californica, *P. andina* Nutt., and *P. brevipaniculata* S. & W. are given as synonyms under *P. Fendleriana*. *Poa brevipaniculata* is very hard to distinguish from *P. Fendleriana* and may well be reduced to synonomy. *Poa californica*, under which name *P. Fendleriana* has been masquerading and under which it is described in the old Coulter's Manual, is an entirely different plant, related to *P. nevadensis* and *P. Buckleyana* and not found in the Rocky Mountain region. *P. andina* Nutt. is also entirely distinct. *P. arida* Vasey and *P. pratericola* Rydb. & Nash were based on *P. andina* Nutt. These two as well as *P. juncifolia* Scribn. are cited by Nelson as synonyms under *P. Sheldonii* Vasey. *P. arida* and *P. Sheldonii* are closely related to each other but *P. juncifolia* is more closely related to *P. laevigata*.

In *Festuca* the following species have been collected in the Rocky Mountains: *F. pacifica* in Utah and Idaho, *F. reflexa* in Utah, *F. megalura* in Idaho, *F. ovina calligera* Piper in Utah, *P. idahoensis* Piper in Idaho, *F. viridula* Vasey in Idaho, and *F. dasyclada* in Utah. *Festuca Thurberi* is one of the best species in the genus, characterized by its long acuminate ligules. It stands in the same relationship to *F. campestris* and *F. scabrella*, as *Poa longiligula* does to *Poa Fendleriana* and *P. brevipaniculata*.

I regard the subgenus *Hesperochloa* of *Festuca*, proposed by Piper, as representing a distinct genus and here propose it as such.

HESPEROCHLOA (Piper) Rydb. gen. nov.

Festuca subgenus *Hesperochloa* Piper, Contr. U. S. Nat. Herb. **10**: 10. 1906.

Densely tufted dioecious perennial, occasionally stoloniferous. Inflorescence a narrow panicle. Spikelets turgid, 3–5-flowered; rachilla scabrous on the basal half. Empty glumes 2, broadly lanceolate, subscarious, shining, the lower 1-nerved, the upper 3-nerved. Floral glumes ovate, acuminate, rounded on the back, faintly nerved. Petals scabrous-ciliate on the keels. Styles obsolete; stigmas hispidulous on all sides, not plumose; ovary deeply sulcate near the apex, sparsely hispidulous; grain beaked and bidentate at the apex.

Hesperochloa Kingii (S. Wats.) Rydb. comb. nov.

Poa (*?*) *Kingii* S. Wats. Bot. King Exped. 387. 1871.

Festuca confinis Vasey, Bull. Torrey Club **11**: 126. 1884.

Festuca Kingii Scribn. U. S. Dept. Agr. Agrost. Bull. 5: 36. 1897.

Not *Festuca Kingiana* (Endl.) Steud. 1855.

Festuca Watsonii Nash, Britt. Man. 148. 1901.

This was originally described as a doubtful *Poa* and afterwards transferred to *Festuca* because the floral glumes are rounded on the back. There are, however, certain characters in the stigmas and the grains that make it fit poorly in either genus. In both *Poa* and *Festuca* the stigmas are plumose, that is, the branches are spreading bilaterally, while in *Hesperochloa* the short bristlelike branches stand out in all directions, a condition rather rare among the grasses.

Hordeum caespitosum Scribn. is found locally throughout the range, *H. montanense* was described from Montana, *H. murinum* and *H. Aegiceras* have been introduced and are locally established especially in Utah.

Sitanion Raf. is a very perplexing genus, and it is very doubtful if the many species proposed by J. G. Smith can be upheld. It is evident that *S. longifolium* and *S. brevifolium* are but local forms of one species, depending on the amount of moisture. As this species is the only one found anywhere near the type locality of

S. elymoides Raf., I think that the latter name should supplant the other two. *S. lanceolatum* J. G. Smith from Montana and *S. marginatum* Scribn. & Merrill from Wyoming are the two species of the range best differentiated and seem to connect the genus with *Elymus*. *S. insulare* was described from northeastern Utah, and *S. ciliatum* has been collected in Wyoming.

ARACEAE

This family is omitted altogether in the New Manual, although *Acorus Calamus* is recorded in my Flora of Colorado and *Lysichiton camtschatcense* (L.) Schott in my Flora of Montana. The former has also been collected in Montana by Butler.

LEMNACEAE

Lemna perpusilla Torr. is included by Nelson in his Manual with the remarks: "Frequent; northern Wyoming to New York." So far as I know this is wholly an eastern species. Specimens so labeled from the Rockies, which have come under my observation, are *L. minor*, *L. minima*, or *L. cyclostasa*, which all have been confused with it.

COMMELINACEAE

Professor Nelson admits two species of *Tradescantia* and gives the following key:

Freely branched; filaments folded; ovary pubescent in riblike lines. 1. *T. laramiensis.*
Simple; filaments straight; ovary pubescent at the apex. 2. *T. occidentalis.*

If these characters hold, as to separating the two species known to Professor Nelson, the second one is not *T. occidentalis*, for the specimen designated by Dr. Britton as the type of *Tradescantia virginica occidentalis*, viz., *Rydberg 1380*, from Thedford, Nebraska, has a branched stem and an ovary pubescent not only at the apex but almost to the base. It is not exactly like the type of *T. laramiensis*, however, for the lateral branches are shorter than the stem proper, the sepals are broader, the leaves broader, and the plant more glandular. In *T. laramiensis* the lateral branches about equal the stem, giving the plant a flat top. If these are specific characters, I do not know. If the two species of the New Manual are distinct, the second one should bear the name *T. universitatis* Cockerell, for it was this form that Professor Cockerell described.

Under the second species is given the following synonym and remark: "(*T. scopulorum* Rose, Contr. U. S. Nat. Herb. **5**: 205. 1899, as to the specimens from Colorado and northward)." This would have been correct if the word "mainly" had been inserted, for I have seen at least one specimen from Colorado that I refer without hesitation to *T. scopulorum*.* The latter differs from the other species of the region by its glabrous or nearly glabrous sepals, its smaller petals, only 10 mm. long, and its subglobose capsule. There is also another species, which should have been included, viz., *T. bracteata* Small, the type of which was from the Black Hills.

MELANTHACEAE

Tofieldia occidentalis S. Wats. has been collected in Idaho; *T. coccinea* Richards. in the Canadian Rockies; *Stenanthella occidentalis* and *Veratrum Eschscholtzianum* in Montana and Idaho.

To me both *Zygadenus dilatatus* Greene and *Z. alpinus* Blankinship seem to be but synonyms of *Z. elegans* Pursh or *Anticlea elegans* Rydb. *Anticlea porrifolia* (Greene) Rydberg (*Zygadenus porrifolius* Greene) was collected last summer in southeastern Utah. So also an undescribed species:

Anticlea vaginata sp. nov.

Perennial, growing in big clumps; cormlike rootstock fully 2 cm. thick; stem 7–10 dm. high, at the base covered with numerous scarious sheaths; leaf blades linear, 3–7 dm. long, 6–10 mm. wide, with numerous veins; inflorescence paniculate, branched; lower bracts linear or subulate, 3–6 cm. long, green, the upper ones ovate, 5–10 mm. long, white; pedicels 5–10 mm. long, often recurved; petals and sepals white, elliptic, obtuse, 7–8 mm. long, usually 7-nerved, the former sometimes a little longer than the latter; filaments linear-subulate, broad at the base, white, slightly shorter than the sepals; anthers nearly round; styles slightly exceeding the perianth, curved.

This differs from the other species of *Anticlea* in its habit of growing in big clumps, and in its numerous loose sheaths at the base of the stem. In the perianth segments it resembles *A. coloradensis*, and *A. porrifolia* in the few veins, the segments are smaller than in the former and broader than in the latter. It resembles

* Garrett and myself collected it also in southeastern Utah last summer.

also *A. porrifolia* in the branched inflorescence but has shorter pedicels and broader leaves. *A. vaginata* grew in loose rich soil under overhanging canyon walls.

UTAH: Armstrong Canyon, near the Natural Bridges, August 4–6, 1911, *Rydberg & Garrett 9407* (type in herb. N. Y. Bot. Gard.).

Professor Nelson gives *Zygadenus gramineus* Rydb. as a synonym of *Z. venenosus* S. Wats. It is evidently *Z. gramineus* he described, although some modification was made. *Z. venenosus* is not found in Wyoming, the most eastern stations known are in the Snake River Valley of western Idaho. It is characterized by the long-clawed petals and sepals and the thick gland. Professor Piper, some years ago, criticized me for redescribing *Z. venenosus*. I think he referred to *Z. intermedius* Rydb. After some arguments on both sides he said that he would look up Watson's type. I do not know that he did, but evidently he came to the same conclusion as I, for in his Flora of Washington* he limited the range of *Z. venenosus* to "British Columbia to California" and hence excluded the Rockies. I have also been criticized for the same thing by Mr. M. E. Jones. Mr. Jones† remarked: "Part of his type of *Zygadenus intermedius* is my No. 2091 from Farmington, Utah. These specimens have no distinct sheath to any of the leaves, except the basal ones. . . . This is a fair sample of Rydberg's accuracy in dealing with *Zygadenus*. . . ." Turning to my original paper,‡ one may see that *J. H. Sandberg 10564* is expressly designated as the type and not *Jones 2091*, which I included in the species. I do not know what Mr. Jones' own specimens show, but there are two of Jones' specimens from Farmington distributed under the number *2091* in the Columbia University herbarium and in these even the upper leaves show short sheaths. One leaf attached near the middle of the stem shows a sheath 1.5 cm. long. I do not think that the presence or absence of a sheath on the upper part is a specific character, but this as well as the citing of a wrong type shows that Mr. Jones is not more accurate than I am.

For my part, I think that *Z. gramineus* can not be upheld as a

* Contr. U. S. Nat. Herb. 11: 198. 1906.

† Contr. West. Bot. 12: 77. 26 Mr 1908.

‡ Bull. Torrey Club 27: 536. 1900.

species distinct from *Z. intermedius*, being a dry hill state of the same with smaller flowers and narrower leaves. *Z. falcatus* Rydb., which Nelson reduced to a synonym, I think is perfectly distinct and nearer related to *Z. paniculatus*. It is what has been known as *Z. Nuttallii* from Colorado. The latter is not found in the range and should have been excluded.

I have here used the name *Zygadenus*, as the species were first described under that name. I have shown that this name belongs to *Z. glaberrimus* and that the plants here discussed should be known as *Toxicoscordion*.

JUNCACEAE

The following species of *Juncus* are found in the Rockies: *Juncus uncialis* Greene, *J. Jonesii* Rydb., *J. Regelii* Buch., *J. Tracyi* Rydb., and *J. mexicanus* in Utah; *J. columbianus* Coville and *J. Regelii* Buch. in Montana; and *J. arizonicus* in Colorado. Professor Nelson includes Colorado in the range of *J. ensifolius* Wikstr. I have seen no specimens of it from that state. The best character, beside the difference in the number of stamens, by which one can distinguish this from *J. saximontanus*, is that the scarious margin of the leaf sheaths in the latter ends in a small auricle, while in *J. ensifolius* the margin gradually diminishes and disappears in the blade.

ALLIACEAE

DIPTEROSTEMON gen. nov.

Plants with fibrous-coated bulbs, few basal elongated narrow leaves and naked scapes. Flowers in subcapitate umbels; bracts 3–5, membranous, colored, usually purple; perianth funnelform or campanulate, purple; segments united about half their length; lobes elliptic, ascending; stamens six; filaments subulate, adnate to the tube, becoming distinct at the throat; those opposite the sepals naked; those opposite the petals at the base with two lanceolate wings or lobes, surpassing the anthers; anthers basifixed; capsule ovate, 3-locular; cells many-seeded.

Some of the species formerly included in *Brodiaea* and lately in *Dichelostemma* differ from the rest enough, I think, to deserve generic rank. The type of *Brodiaea* is *B. grandiflora* Smith. This is the same as *Hookera coronaria* Salisb., published a few

months earlier. As the latter is the type of *Hookera*, *Brodiaea* becomes a pure synonym. Dr. Greene,* who was the first to segregate into genera the members of *Brodiaea* taken in the sense of Dr. Watson, retains both genera. Evidently he regarded Smith's second species, *Brodiaea congesta*, as the type. This can scarcely be done, as *B. grandiflora* is not only the first species, but it is more extensively described and discussed. Greene himself afterwards discarded *Brodiaea* and adopted *Dichelostemma*, proposed by Kunth on *Brodiaea congesta* Smith. Alphonso Wood had extended Kunth's genus to include also *B. capitata* Benth. and *B. volubilis* Baker (*Stropholirion californicum* Torr.). Wood was followed by Greene in including these species in the genus. *Stropholirion* has been generally recognized as a genus, even by S. Watson. The typical species of *Dichelostemma*, i. e., *D. congesta* (Smith) Kunth and its relative *D. multiflora* (Benth.) Heller, have only 3 stamens alternating with 3 staminodia and differ from the typical species of *Hookera* only in the rounded base of the perianth and the subcapitate inflorescence. If they are kept distinct then *Seubertia* should be regarded distinct from *Triteleia*. *Brodiaea capitata* has 6 fertile stamens with subulate filaments. At the base of each of the inner three there are two lanceolate lobes partly adnate to the perianth, forming together a crown of 6 instead of 3 members. To the new genus proposed here, belong:

Dipterostemon capitatus (Benth.)

Brodiaea capitata Benth. Pl. Hartw. 339. 1857.

Dipterostemon pauciflorus (Torr.)

Brodiaea capitata pauciflora Torr. Bot. Mex. Bound. Surv. 218. 1859.

Dipterostemon insularis (Greene)

Brodiaea insularis Greene, Bull. Calif. Acad. Sci. **2**: 134. 1887.

Dipterostemon pulchellus (Salisb.)

Hookera pulchella Salisb. Parad. **2**: *pl. 117*. 1808.

NEW YORK BOTANICAL GARDEN.

* Bull. Calif. Acad. Sci. **2**: 125–144. 1886.

Sexual fusions and spore development of the flax rust

FRED D. FROMME

(WITH PLATES 8 AND 9)

The variations found in different species of rusts so far investigated as to their sexuality, have made evident the desirability of further investigating a large number of forms, if we are to arrive at a definite understanding of the sexual processes in the Uredineae in general. From this standpoint I have taken up the study of the flax rust, *Melampsora Lini* (Pers.) Desm. The caeoma type of aecidium has in all cases proved favorable for the study of sexual fusions. The flax rust is no exception in this respect, and the abundance of the fusion stages in my material leaves little to be desired. Dr. E. W. Olive suggested the problem to me, and the results here recorded were largely worked out under his direction at Brookings, S. Dak.

A summary of the literature prior to 1908 has been given by Olive ('08) and still more recently by Maire ('11), so that the later papers only will be discussed here. While the sexual nature of the fusions in the rusts may be regarded as definitely established, the morphological character of the two cells involved and the phylogenetic significance of the process are still points of contention. Two more or less distinct types of fusion have been recognized. (1) A "partial cell fusion" where fertilization is effected by the migration of the nucleus of a vegetative cell into a special "fertile cell," as found by Blackman in *Phragmidium violaceum*. (2) A complete cell fusion between equal gametes, as figured by Christman in *Phragmidium speciosum* and suggested for *Uromyces Caladii* and *Caeoma nitens*. This type of fusion was later substantiated by Blackman in *Melampsora Rostrupi*, and by Olive in *Triphragmium Ulmariae* and *Gymnoconia interstitialis* (*Caeoma nitens*). Both of these processes Blackman considers as reduced types of fertilization that have supplanted a true fertilization, in which the spermatia functioned as male cells and

the "sterile cells" above the "fertile" or female cells as trichogynes. On this view the Uredineae are derived from the red algae. Christman considers the "fusion of equal gametes" as a true fertilization in which a "non-resting zygospore" is produced. He suggests that the nuclear migrations of Blackman may be pathological in nature like similar migrations observed by him in the teleutosorus of *Puccinia Podophylli*. The sterile cells are merely "buffers" and the spermatia may be degenerate gametophytic conidia. Christman has also found a fusion of equal cells in the formation of the primary uredospores in *Phragmidium Potentillae-canadensis*, thus showing the morphological equivalence between the primary uredospores and aecidiospores.

Olive, in his 1908 paper, described a further series of forms: *Triphragmium Ulmariae*, *Gymnoconia interstitialis* (*Caeoma nitens*), *Phragmidium Potentillae-canadensis* and the microform *Puccinia transformans*. He also studied nuclear divisions in three other species: *Uromyces Scirpi*, *Uromyces Lilii*, and *Puccinia Cirsii-lanceolati*. *Triphragmium Ulmariae* has a crustlike primary uredosorus very similar to that of *Phragmidium Potentillae-canadensis*, studied by Christman. In this form Olive finds numerous cases of wide open cell fusions of the type described by Christman. The fusion pores, however, may be of varying diameters. In most cases they are broad, the intervening cell walls being entirely absorbed, but occasionally the pore is narrow so that the nucleus is constricted somewhat in passing. He found no cases, however, where the nucleus is drawn out in a fine thread in passing through an imperceptible pore as figured by Blackman. He further observed, that although the fusing cells may be placed side by side in the same plane, as Christman found them, one of the gametes is perhaps more often found to lie somewhat below the other. In such instances only the upper of the fusing cells appears to have cut off a sterile cell. When the two gametes are not in direct contact a very short conjugation tube may apparently be formed (*fig. 26*). In all cases figured in *Triphragmium*, only one of the fusing cells enlarges and becomes the basal cell. This method of forming the basal cell is quite different from that described by Christman for *Phragmidium Potentillae-canadensis*, where the fusing cells combine to form the basal cell.

The subsequent budding off of the primary uredospores in a fashion similar to that described by Christman confirms his evidence that the primary uredospores and aecidiospores are morphologically equivalent. Although Christman did not find the fusion stages in *Caeoma nitens*, his material being rather old, Olive figures two cases (*fig. 35* and *36*) for this form, where the fusion occurs between cells placed adjacent and parallel, similar to Christman's figures of *Phragmidium speciosum* but without showing sterile cells. He also figures a third case where the nucleus of one cell is passing into a cell placed immediately above it but belonging to a distinct hypha. This as he points out is very similar in appearance to Blackman's ('04) *fig. 66* and *68*. *Fig. 34* and *36* were drawn from the same section and were but a short distance apart. This instance, in conjunction with his observations on *Triphragmium*, convince him that Blackman's "nuclear migrations" and Christman's "fusion of equal gametes" may occur in the same rust and in the same pustule. Sexual fusions may begin through a pore which is narrow at first so that the nucleus is constricted in passing. Later this pore may broaden and the entire contents of the two cells fuse. He would distinguish between such cases and cases of undoubted pathological migrations such as he finds between the multinucleated cells of the aecidium of *Puccinia Cirsii-lanceolati*. In the typical microform, *Puccinia transformans* on *Tecoma stans*, fusion is shown in the teleutosorus between the end cells of two hyphae in one instance, while in another the end cell of one is fusing with the penultimate cell of the other. The fusions here are immediately followed by growth which results in teleutospores borne on several binucleated cells. The sporophyte generation in this case consists, then, of only a few, three or four, cells. In *Uromyces Scirpi* and *Puccinia Cirsii-lanceolati*, as well as in some eight other species, he found one or more large multinucleated cells at the base of the young aecidium cups. He is inclined to interpret these as sporophytic cells in which nuclear division has proceeded faster than cell division, due possibly to the stimulus to growth derived from the sexual act. He suggests the possibility that the solution of the problem as to the development of the aecidium cup with its peridium and apparent centralized structure may be found in these multinucleated cells. Es-

pecially striking were the cases found in *Puccinia Cirsii-lanceolati*. Fifteen nuclei in a single cell were figured in one instance. From his study of *Triphragmium* and other forms, Olive concludes that only one of the gametes ordinarily bears a sterile cell and that one gamete generally lies somewhat below the other. This leads him to believe that the two gametes differ somewhat in the time of their development. The first hyphae to form the upright layer under the epidermis do not fuse among themselves but cut off sterile cells and are fertilized by the tip cells of hyphae that push up later from below. Olive does not differentiate these cells as "fertile and vegetative," as Blackman has done, but believes they are entirely equal in size and contents and differ only in time of development. He agrees with Christman that the sterile cells are merely "buffers" and cannot be considered phylogenetically as trichogynes.

In two shorter articles, published earlier in the same year ('08), Olive calls attention to the similarity between the multinucleated cells, which he found at the base of a number of young aecidium cups, and the archicarps of De Bary, Massee, and Richards. He thinks it quite probable that the basal cells of the aecidium are the ultimate branches of these multinucleated cells. The cup type of aecidium was probably derived from the more simple caeoma type. He has found as many as six nuclei in a fusion cell of the caeoma type, due probably to nuclear division proceeding faster than cell division, and points out that a still further development of such a cell coupled with partial suppression of other neighboring cell-fusions, especially in a deep lying caeoma, might give rise to the cupshaped type of aecidium.

Kurssanow ('10) reinvestigated *Puccinia Peckiana* (*Caeoma nitens* of Christman and *Gymnoconia interstitialis* of Olive). He agrees with Christman in all essentials. The conjugation is between entirely similar gametes. Sterile cells are normally formed from both conjugate cells, but these have degenerated or have been lifted off by the rupture of the epidermis before the time of fusion. These are mere "buffer" cells and cannot be interpreted as trichogynes. Kurssanow does not accept Olive's attempt to harmonize the observations of Blackman and Christman. Either the two methods of conjugation are limited to the

different forms studied, or Blackman's "partial cell fusions" must be regarded as pathological in nature. Kurssanow has also observed undoubted pathological migrations in his material aside from the normal conjugations.

Maire ('11) has reviewed the numerous problems in the study of the Uredineae and given a résumé of our present knowledge of the cytology of the group. He regards the sexual fusions as well established for forms possessing an aecidium. In reexamining his preparations of *Puccinia Bunii*, an opsis form, he has been able to find the isogamous fusion of two cells to bring about the formation of the primary "synkaryocyte" but is not able to see the stages clearly. He does not regard the question of the isogamous or heterogamous nature of the fusion as of great importance and thinks cases may be found of the union of sister cells or even confirmation of the method of forming a binucleated cell originally described by Sappin-Trouffy and later by Maire, in the microform, *Puccinia Liliacearum*. Maire holds that the present sexual fusions have replaced a primitive sexuality analogous to that in the red algae, in which the spermatia functioned as male cells. The interpretation of the sterile cell as a trichogyne he considers as extremely hypothetical. He holds that the Uredineae and the Basidiomycetes have a common origin, but the latter have perhaps lost all trace of sexuality. He favors the view that the primitive rust forms had spermatia and teleutospores only, and that the aecidiospores and uredospores have been intercalated in the life history to provide for rapid distribution.

Olive, in a recent paper ('11), has also discussed the character of the primitive rusts and the origin of heteroecism. He also holds to the theory that the more complex types were derived from the simpler lepto- and microforms by a progressive development of the sporophyte. This is substantiated by analogy with the higher plants. The primitive forms were probably autoecious. The alternation of hosts was made possible by the production of aecidiospores which are invigorated by the stimulus derived from the sexual act and therefore better able to make the transition to a new host than the uninucleated sporidia. This would mean that the present hosts of the gametophytic stage of the rusts (aecidium), of the heteroecious forms, were the hosts of the original

autoecious ancestors. The prevalence of heteroecious forms with pleophagous sporophytes and the fewness and evident close relationship of the hosts of the aecidial stages in these cases, as well as the multiplicity and remote relationship of the hosts of the sporophyte, support this conclusion.

Melampsora Lini is quite abundant on cultivated flax, *Linum usitatissimum*, in the vicinity of Brookings, S. Dak. A considerable quantity of rusted flax straw was collected in the fall of 1910 and was exposed during the winter in a cloth bag suspended from a window. In the spring a small plot was sown to flax and the rusted straw scattered over the plot. This was watered frequently and numerous infections were obtained, the sori appearing when the young plants were about five inches high. These sori are quite small and it is difficult to distinguish spermogonia from aecidia. Small portions of the leaves and stems were fixed in Flemming's medium fixing solution, imbedded, sectioned, and stained with Flemming's triple stain and Bendas' iron haematoxylin. Sections of the uredo- and teleutosori were kindly furnished me by Dr. Olive from material previously prepared by him.

Melampsora Lini is an autoecious eu-form, i. e., the complete series of spore forms, spermatia, aecidia, uredo, and teleuto, are all borne upon the common host, flax. The aecidium is of the caeoma type, which has been found most favorable for the study of cell fusions, and the teleutospores show the nuclear fusions very clearly.

SPERMOGONIA

These are rather inconspicuous in color and occur on both sides of the leaves and occasionally on the stems. They are produced only by infections with sporidia. They are typically flaskshaped, without ostiolar filaments and are placed subepidermally. Sometimes the spermogonium is merely a diffuse layer of spermatiophores without a definite flasklike structure. Several of these spermogonia may occur in the same localized area but they are seldom confluent. Their frequent close association with the aecidia will be discussed in connection with the development of the aecidium. The spermatiophores from which the spermatia are abstricted arise from large rectangular cells which are arranged in a regular series at the base of the spermogonium. The sper-

matiophores differ from those described by Blackman in that they are divided into a number of uninucleated cells, usually four, each of which puts out a fingerlike process from its upper end on the tip of which a single spermatium is produced. See FIG. 1 and 2. The spermatiophores of *Gymnosporangium clavariaeforme* and *Phragmidium violaceum*, as described by Blackman, are single elongated, uninucleated cells. The single nucleus divides successively to form the nuclei for a number of spermatia which are abstricted from the elongated fingerlike tip of the spermatiophore. FIG. 4 shows two spermatia fully formed while a nucleus still remains in the base of each cell. This seems to indicate that two or more generations of sporidia are produced from the same cell of the spermatiophore.

AECIDIUM

The aecidium arises from a uninucleated mycelium, which in the vegetative condition cannot be distinguished in any way from that which produces spermogonia. It is confined chiefly to the intercellular spaces of the host. The nuclei at this stage are rather small but exhibit a clearly defined chromatin network and a definite nucleole. After a period of vegetative development the filaments grow up between the cells of the mesophyll and reach the epidermis. Here they branch laterally to form a weft of hyphae. The branches next push up vertically and form a sort of palisade of large cells which contain very large nuclei and more compact cytoplasm than the ordinary vegetative cells. See FIG. 5. Each cell now divides somewhat unequally, producing a smaller cell above, which again divides so that two smaller cells are formed above a single larger cell. See FIG. 5. The larger cells are the future gametes and at this stage form a rather even dense layer below the two sterile cells. The shape of the sterile cells is determined by the pressure of the epidermis and that of the surrounding cells. When they press directly against the epidermal cells they are flattened laterally and the upper cell conforms to the outline of the overlying epidermal cell. At other points where the pressure is not so direct they may be somewhat elongated. In either case they soon become vacuolate and disappear usually by the time of sexual fusions. These are the "buffer" cells of Christman, and we see that they are here in two layers instead of a

single layer as he found in *Phragmidium speciosum*. The entire sorus at this time is a group of vertically placed hyphal branches without pseudoperidium or paraphyses. It cannot be considered as a unit in any proper sense but rather as a collection of reproductive units. The development of the sorus proceeds in a more or less centrifugal fashion, the older branches being found at the center while the younger are at the outer borders of the group. The various stages in the degeneration of the sterile cells are well seen in passing from the outer borders toward the center. Christman's interpretation of these sterile cells as "buffers" seems entirely adequate, as their function is evidently a protective one. They relieve the pressure of the epidermis on the underlying reproductive cells and then degenerate to provide room for the subsequent development of the latter. As noted, in all the forms so far investigated only one layer of sterile cells has been observed, while in *Melampsora Lini* two layers of sterile cells are normally produced. In his investigation of *Melampsora Rostrupi*, Blackman occasionally found a double layer of short crushed cells lying above the fused cells, but owing to the age of his material he did not note the method of their formation. In view of the facts above described it seems quite reasonable to assume that Blackman's observation shows that a similar condition is found in *M. Rostrupi*. It is possible that all the Melampsoras develop their gametes at a deeper point in the sorus than the more superficial caeomas of the *Phragmidium* type.

The frequent intimate association between the spermogonia and aecidia, referred to above, is an interesting feature of the flax rust. In rusts bearing both spermogonia and aecidia the former usually precedes the latter in time of development by a period of several days or weeks. In this form, however, a marked difference in time of development does not exist. In general the spermogonia appear somewhat earlier than the aecidia, but they are often found developing simultaneously and intimately associated. Spermogonia may bound the aecidium on either side or may even be included in it. It is very difficult to trace the origin of the mycelium from which the two sori arise on account of the interweaving of the hyphae, but there is no sharp boundary between the two and they cannot be distinguished in the vege-

tative condition. It seems quite probable that they arise from common points and that branches from the same mycelium may form both kinds of sori. The aecidium and spermogonium are frequently separated only by the outer sterile layers of the spermogonium. Their development proceeds simultaneously, spermatia and aecidiospores being formed at the same time and often found lying in the same cavity under the epidermis. Sometimes the spermatia are already present when the aecidium has just reached the stage of sexual fusions. One of the difficulties in assuming that the spermatia are male cells has been the inaccessibility of the cells of the aecidium to fertilization by them and the production of the spermatia prior to the development of the aecidium. Here we have a case, however, where the two develop at the same time, and so near together that fertilization might easily be accomplished.

The large vertical cells of the aecidium now begin to conjugate in pairs. This conjugation is brought about by an absorption of the intervening cell walls at the area of contact. The upper portions of the cells involved are usually in contact so that the absorption takes place in this region. See FIG. 7. The lower portions of the cell walls are usually not absorbed and the fusion cells formed remain with a conspicuous two-legged base. At the time of fusion the cytoplasm of the gametes is quite dense and stains readily, consequently they stand out quite sharply differentiated from the vegetative cells below, which have lost most of their contents. They can readily be distinguished under the low powers of the microscope without the aid of the oil immersion. Sometimes the tips of the gametes converge and the point of contact and absorption is at the center, as in FIG. 8. The area absorbed may be of varying diameters, as Olive holds, but the passage of a nucleus through an imperceptible pore has never been observed in the case of the true fertilizations. Certain cases of nuclear migrations which are apparently of an abnormal nature, will be referred to later. The fusing gametes do not always lie side by side at the same level in the sorus. They may meet at various angles, and frequently one of them lies somewhat below the other. See FIG. 9. I do not believe, however, that in *Melampsora Lini* this indicates a difference in the time of develop-

ment of the gametes, as Olive finds for *Triphragmium Ulmariae*. In the early stages of the sorus the gametes are not always placed in an even parallel layer but may vary in elevation. The irregularities due to the loose indefinite nature of the caeoma quite fully account for the unequal position of the gametes. The presence or absence of sterile cells at the time of fusion, again does not seem a good criterion for determining the relative age of the two gametes. I have observed several cases where both gametes at the time of fusion still have two sterile cells intact. See FIG. 10. As I have pointed out, however, these sterile cells have usually disappeared at the time of fusion.

The abundance of sexual fusions in *Melampsora Lini* is most striking. The sexual fusions figured by earlier students have been scattered and disconnected and apparently only occasionally found. In my material I have sections showing practically every pair of gametes in the sorus in some stage of fusion. These stages are so abundant that there can remain no doubt whatever that the binucleated condition in this form is always instituted by means of a cell fusion between entirely equivalent gametes. FIG. 11 shows a collection of "fusion cells" that were especially well situated for drawing. A triple cell fusion is shown in the center of the group with three ordinary fusions on either side. The "fusion cells" are rather old here, one or more aecidiospores having been produced in most cases, but the double "basal cells" still show the original fusions distinctly. FIG. 12 shows another series of cell fusions. The five pairs of gametes in this instance are of about the same age as those shown in FIG. 11. Younger pairs are shown in FIG. 13. The gametes on the left have just completed the fusion while those on the right have cut off the first aecidiospore mother cell. FIG. 14 shows a mature, binucleated aecidiospore with a chain of intercalary cells and young aecidiospores ending in a double cell fusion below. The process by which the chain of spores and intercalary cells are formed has been fully described and need not be taken up here.

As previously mentioned, Olive has figured a somewhat different method of forming the "basal cell," in *Triphragmium Ulmariae*, from that shown by Christman in *Phragmidium Potentillae-canadensis* and *P. speciosum*. As found by Christman, the

"basal cell" is formed by the equal enlargement of the two fused cells, and the aecidiospore mother cell lies directly over the fused cells. The cases figured by Olive, on the other hand, show that the nucleus of one gamete passes into the other, and the gamete which is now binucleated elongates and functions directly as the "basal cell." Cases of this nature also occur in *Melampsora Lini.* It will be seen in the fusion shown in FIG. 15 that the gamete on the right has elongated and become the "basal cell" and has cut off the first aecidiospore mother cell. The nucleus of the gamete on the left lies in the opening between the two fused cells. A comparison of this figure with FIG. 13 and 14, which are cases of equal contribution to the "basal cell," will illustrate the difference between these two methods. It is interesting to find both of these methods occurring here in the same rust.

Reference has already been made to a triple cell fusion, shown in FIG. 11, which lies in the center of a group of ordinary cell fusions. There can be no question that the condition there shown has been brought about by the fusion of three gametes instead of two. FIG. 16 shows an early stage of a triple cell fusion. The intervening cell walls are absorbed just as in the case of a double cell fusion, and a "basal cell" is produced which contains the nuclei and cytoplasm of three gametes. FIG. 17 is a case of a triple cell fusion where the three-legged base is especially distinct. These triple fusions are of comparatively frequent occurrence in my material. FIG. 18 (PLATE 9) shows a triple fusion which presents a still further complexity. It will be seen from the figure that two adjoining cells in the same filament on the right have fused with a single cell in another filament on the left. This has also resulted in a trinucleated "basal cell" but differs from the usual triple fusions in that two of the gametes come from the same filament. I have observed several other cases of this nature. It seems, then, that not only a single layer of gametes are produced, in this form, but occasionally another cell placed below the ordinary functional cells also has the capacity for effecting fertilization. The three nuclei thus associated in the same "basal cell" probably divide "conjugately" to produce trinucleated aecidiospores. FIG. 19 shows a trinucleated aecidiospore mother cell which has just been formed by the division of the trinucleated "basal cell" on which

it is borne. A later stage is shown in FIG. 20. The trinucleated spore at the top of the chain has cut off a small intercalary cell while the spore mother cell just below is as yet undivided. FIG. 21 shows a mature aecidiospore which contains three nuclei. Such spores are frequently found lying free in the cavity under the epidermis among the ordinary binucleated type. A mature aecidiospore containing six nuclei was also found. See FIG. 22. This condition might have been brought about by the division of three original nuclei without the formation of the intercalary cell.

Cell fusions between four gametes are sometimes found along with the two- and three-celled types but are relatively infrequent. I have observed only three well-defined cases of this nature. Two of these cases are shown in FIG. 23 and 24. The four cells that have participated in the fusion can be seen distinctly, but the cell contents were stained so strongly that the nuclei could not be distinguished.

Still more striking are the large multinucleated spore mother cells which are occasionally found in the aecidium. One of these, FIG. 25, contains eleven nuclei. The cell is being divided by an ingrowing cell wall near the center. The uneven number of nuclei is probably due to the sectioning, but it is impossible to locate it with certainty on the next section. Another of these large structures is shown in FIG. 26. The evident pairing of the eight chromatin masses indicates that a division of four nuclei is just being completed. The base of the cell is indistinct and I am not able to determine its origin. FIG. 27 shows a case of a completed division of a four-nucleated cell forming a distinctly four-nucleated aecidiospore and an intercalary cell in which the nuclei are less distinct but evidently four in number. It seems quite probable that the conditions shown in FIG. 26 and 27 have resulted from an original four-cell fusion. Attention has been called to Olive's observation of large multinucleated cells at the base of certain young aecidium cups especially in *Puccinia Cirsii-lanceolati*. He was inclined to interpret these as sporophytic structures resulting from the greatly stimulated growth following sexual fusions. Whether these are really central organs from which the aecidium develops, has not been established. There is

perhaps some similarity between them and the multinucleated cells that I have found.

I have examined my material carefully to determine whether the binucleated condition is ever brought about by the migration of the nucleus of one cell into an adjoining cell, as described by Blackman, and have found no such cases in the fertile layer of the aecidium, or such as could be considered true fertilizations. Occasionally, however, in the vegetative mycelium below the fertile layer of the aecidium, I have found cases that are very similar in appearance to some of Blackman's figures. One of these is illustrated in FIG. 28. The nucleus here is evidently passing through a very small pore in the walls between two adjoining cells and is drawn out in a very fine thread in the passage. The two cells are small, contain but very little cytoplasm, and lie some distance below the surface of an old sorus which has already produced aecidiospores in the regular manner. Another case of migrations of nuclei is shown in FIG. 29. Two nuclei from neighboring vegetative cells are migrating into the same vegetative cell. It does not seem possible to connect any of these cases with the normal process of fertilization in any way, and the interpretation of Christman, Olive, and Kurssanow of similar phenomena as "pathological" seems most natural.

UREDO

The uredosori arise from a binucleated mycelium which results only from infections with aecidiospores. They are found on both sides of the leaves and on the stems. The sori are indefinite in extent, without pseudoperidium or paraphyses except for a few sterile, capitate filaments, which sometimes occur at the outer borders of the sorus and less frequently are interspersed among the spores within the sorus. The uredospores are borne upon long stalks which are made up of two or three elongated cells. See FIG. 30. They are large, ovate to elliptical in form, and contain two nuclei, as do all of the stalk cells upon which they are borne. The walls are thin and finely and evenly verrucose with low papillae and equatorial, rather indistinct germ pores. The sterile filaments, commonly called paraphyses, which are found among the spores, are long and extremely slender and terminate

in somewhat irregular knoblike cells, which are usually somewhat larger that the uredospores. The walls are somewhat thicker than those of the uredospores and perhaps a little smoother, although the older ones are roughened like the uredospores. Young paraphyses were found to contain two nuclei at the base of the apical knob. See FIG. 30. The stalks were undivided and very slender and contained but very little cytoplasm. The nuclei evidently degenerate very rapidly, as in the older filaments they have disappeared entirely. Of the cytoplasmic contents only a few shriveled threads remain. The nature of these sterile filaments is perhaps not entirely clear, but the observation that they are binucleated when young suggests that they have a common origin with the functional uredospores.

TELEUTO

The teleutospores appear later in the season than the uredospores and are associated with the ripening of the flax. The sori are found on both sides of the leaves and more frequently on the stems. They are sometimes round and isolated but are more often confluent in long areas, which are reddish brown when young and become quite black when old. The spores are of the elongated one-celled type of the Melampsoras and are cemented together above in a firm, waxy layer. See FIG. 31. They are sessile on the short cubical cells at the base of the sorus, which lose their contents with the development of the teleutospores. The young teleutospores are binucleated but soon become uninucleated through a fusion of the two nuclei into one. Occasionally a secondary layer of teleutospores forms an overgrowth above the first. This is apparently brought about by the growing up of the mycelium around the borders of the primary layer of teleutospores to form a secondary layer of shorter teleutospores above the first.

DISCUSSION

The existence of sexuality in the rusts may be considered as well established for those forms that have the caeoma type of aecidium. The cup type of aecidium, however, needs much further study, though Christman's figure for *Uromyces Caladii* shows that the fusions there are probably essentially similar to

those in the caeoma type, and Olive's multinucleated cells may be correlated with the more definite form and structure of the cup. The double layer of sterile cells in *Melampsora Lini* may possibly be comparable to the pseudoparenchyma of an aecidium cup and indicate a transition between the more superficial caeoma and the deeper cup type of aecidium. The evidence seems to point to the conclusion that the short-cycled micro- and leptoforms are the more primitive and that such a form as the flax rust with its five spore forms is more highly specialized. It is interesting to note that the less differentiated caeoma type of aecidium can persist in these higher types of rusts.

As to the relationships of the Uredineae with other fungi or algae, the preponderance of evidence at present seems to favor the view that the present sexual fusions are a substitute for a more primitive type in which the spermatia functioned as male cells. The existing sexual processes are certainly of a zygosporic character. The conjugation is betwen two entirely similar cells, which participate equally in the formation of a double cell from which a series of spores are produced. This is of course no proof that the primitive form of sexuality was zygosporic. Blackman, as previously stated, would derive the Uredineae from the red algae. While this connection is as yet doubtful, it is perhaps the most plausible view of the origin of the group.

Although Blackman's observation of a "partial cell fusion" by means of "nuclear migrations" in *Phragmidium violaceum* has never been directly disproved, the indirect evidence shown in the equal cell fusions that have been found in all other aecidia of the caeoma type, so far investigated, leads to the conclusion that this form is somewhat aberrant or that the true fertilization has not been observed. The further observations of "pathological" migrations by other investigators and the existence of very similar migrations between vegetative cells of *Melampsora Lini*, which cannot be regarded as true fertilizations, are striking facts. While the area of absorption between two gametes may be small at first and later broaden, as Olive has shown, there still remains a considerable difference between the passage of a nucleus as a fine thread through an extremely small pore, which cannot be seen before or after the passage, and the passage of a nucleus through

a rather small pore which later broadens to permit the entire contents of the two cells to fuse.

The fusions of three and four cells, which are occasionally found in *Melampsora Lini*, are perhaps to be compared with cases of di- or polyspermy in animals. The first beginnings of triple cell fusions are of rather common occurrence in the group of the Conjugatae, but the complete fertile product of such a fusion is at least a rare occurrence. De Bary figures one case in *Zygnema pectinatum* of a completed conjugation between three cells, but the resulting zygospore has not rounded up, as do the zygospores formed by the fusion of two cells, and remains partially distributed in a horseshoe form between the three fused cells. As I have shown, the triple fusions in the flax rust are functional in the production of trinucleated aecidiospores. It would be very interesting to determine whether these spores in turn produce a mycelium with trinucleated cells. Blackman has also observed trinucleated "basal cells," aecidiospore mother cells, and aecidiospores in *Phragmidium violaceum* but did not determine the manner in which this condition is brought about. He observed that the size of these nuclei is usually somewhat less than that of the normal paired nuclei, and suggests that one of the nuclei of a binucleated cell may have divided while the other remained in the resting condition. He also suggests that a migration of two nuclei into one cell would bring about a similar result. In the short-cycled form *Puccinia Malvacearum*, abnormal vegetative cells and teleutospores containing three nuclei were found by Blackman. Triple and even quadruple fusions are certainly to be reckoned with as widespread and fairly common phenomena in the sexual reproduction of the rusts. They show a certain elasticity in the relations of the gametes, which may be further evidence that the sexual process, as at present found, is secondary and highly modified from the primitive condition in the group.

SUMMARY

The spermatia of the flax rust are produced on septate branching spermatiophores, which differ in this respect from the unbranched non-septate spermatiophores described by Blackman for *Phragmidium violaceum* and *Gymnosporangium clavariaeforme*.

This feature may furnish a further basis for use in the classification of the Uredineae.

The fusing cells in the aecidium are entirely similar and form a fairly even series at the base of the sorus. Two short sterile cells are normally formed above each gamete. Their function is evidently protective and they may correspond to the pseudoparenchyma of young aecidium cups. Sexual fusions are very abundant in this form, and many pairs of gametes in various stages of union can be found side by side in the same preparation.

Fusions of three and four cells have also been found in addition to the normal two-cell fusions and are perhaps to be regarded as further evidence that the sexual processes as found in the rusts are of a secondary character. Large multinucleated cells are also present in the same sorus with two-, three-, and four-cell fusions.

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Explanation of plates 8 and 9

PLATE 8

FIG. 1. A branching, septate spermatiophore bearing spermatia on the finger-like elongations of the cells. × 1,500.

FIG. 2. Another branched spermatiophore. The two upper cells have not as yet produced spermatia. The penultimate cell shows the beginning of the fingerlike outgrowth. × 1,500.

FIG. 3. A septate, unbranched spermatiophore. × 1,500.

FIG. 3a. A spermatium. × 2,250.

FIG. 4. A two-celled spermatiophore bearing spermatia. × 1,500.

FIG. 5. A portion of a young aecidium showing a single layer of larger cells, the gametes, with two layers of short sterile cells above and vegetative mycelium below. The upper sterile cells show conformity to the outline of the overlying epidermis. An early stage of fusion is shown between the second pair of gametes from the right. × 1,000.

FIG. 6. A young pair of gametes more highly magnified. Two short, crushed; sterile cells are present above each gamete. × 1,500.

FIG. 7. Cell fusion between two equal and parallel gametes. The upper portions of the intervening cell walls have been absorbed. × 1,500.

FIG. 8. An early stage in the fusion of two gametes. The absorption is at the center of the two cells, as the tips are not in contact. × 1,000.

FIG. 9. One of the gametes lies somewhat below the other. × 1,000.

FIG. 10. Fusion between two gametes, both of which still have two sterile cells intact. × 1,000.

FIG. 11. A group of seven "fusion cells." A triple cell fusion lies in the center of the group with three double cell fusions on either side. One or more aecidiospores have been produced from most of the "fusion cells." × 750.

FIG. 12. A group of five "fusion cells." × 750.

FIG. 13. A pair of younger "fusion cells." The gametes on the left have just completed the fusion while those on the right have cut off the primary aecidiospore mother cell. × 1,000.

FIG. 14. A mature aecidiospore and a chain of intercalary and spore mother cells which have been cut off from the "basal cell" below. × 750.

FIG. 15. Only one of the gametes functions as the "basal cell." The cell on the right has elongated after the fusion and has cut off the primary aecidiospore mother cell. × 1,000.

FIG. 16. An early stage of a triple cell fusion. × 1,000.

FIG. 17. A completed fusion between the tips of three gametes. × 1,000.

PLATE 9

FIG. 18. Another type of triple cell fusion. Two adjoining cells in the same hypha have fused with a single cell on the left. × 1,000.

FIG. 19. A trinucleated spore mother cell borne on a trinucleated "basal cell," which has been formed by a triple cell fusion. × 1,000.

FIG. 20. A trinucleated "basal cell" which has produced the second aecidiospore mother cell. The primary aecidiospore mother cell has divided to form an aecidiospore and intercalary cell. × 1,000.

FIG. 21. A mature trinucleated aecidiospore. × 1,000.

FIG. 22. A mature aecidiospore containing six nuclei. × 1,500.

FIG. 23. A quadruple cell fusion. The "fusion cell" is stained so heavily that the nuclei are not distinguishable. × 1,000.

FIG. 24. Another quadruple cell fusion. × 1,000.

FIG. 25. A large spore mother cell, of the aecidium, containing eleven nuclei. A cell wall is being formed near the center of the cell. × 1,000.

FIG. 26. A cell containing eight paired chromatin masses indicating that a simultaneous division of four nuclei is just being completed. × 1,500.

FIG. 27. A four-nucleated aecidiospore and intercalary cell. × 1,500.

FIG. 28. Migration of a nucleus through the walls of two adjoining vegetative cells which lie below the fertile layer of an old aecidium. × 1,500.

[The nucleus is not as distinct in the plate as in the original drawing, and the disposition of the cytoplasm has been somewhat changed in the reproduction of the figure on the plate.]

FIG. 29. Migration of two nuclei from two vegetative cells into a third vegetative cell. × 1,500.

FIG. 30. A portion of an uredosorus. The binucleated uredospores are borne on long stalks made up of two or three binucleated cells which arise from binucleated mycelium. Sterile, capitate paraphyses are shown at the outer borders of the group. The knoblike apical cell is somewhat irregular in outline and the stalk is non-septate and very slender. The young paraphyse on the right is binucleated and contains a small amount of cytoplasm while the older one on the left has lost its contents. (Slightly diagrammatic.) × 750.

FIG. 31. A portion of a teleutosorus showing the appressed layer of one-celled teleutospores, the tips of which are imbedded in a waxy substance. The spore on the right is binucleated while the others have become uninucleated through a fusion of the primary nuclei. × 750.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1910-1912)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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